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INVASIVE SPECIES II

The effect of newt toxin on an invasive snail

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Abstract Invasive species are well documented to impact native species where they are introduced. In the Santa Monica Mountains, a native species of amphibian, the California newt (*Taricha torosa*) possesses a neurotoxin, tetrodotoxin (TTX) that is considered a chemical defense against predation but also appears to facilitate ecological processes and specifically affect freshwater macroinvertebrate behavior. A recently introduced invasive species, the New Zealand mud snail (*Potamopyrgus antipodarum*), is known to negatively affect ecosystems it invades and means to control its proliferation once introduced are limited. Given the ecological role of newt neurotoxin, we hypothesized that TTX may impact *P. antipodarum* behavior and tested its effects upon snail movement in laboratory assays and in-stream experiments. When snails were exposed to ecologically realistic TTX concentrations and newt chemical cues that contain TTX they moved significantly less and distance was significantly reduced relative to controls. In a natural stream, significantly more *P. antipodarum* moved out of areas exposed to newt chemical cues relative to snails in the presence of native tree frog cues (*Pseudacris cadaverina*). Our results suggest that California newts may help limit the spread of *P. antipodarum* in streams where *T. torosa* is both able to persist and possess adequate chemical defenses.

Keywords New Zealand mud snail · *Taricha* · *Potamopyrgus antipodarum* · Santa Monica Mountains · Los Angeles

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Introduction

Aquatic invasive species can negatively impact native species richness and abundance, outcompete and displace native species, lower local biodiversity, transmit disease, and affect ecosystem dynamics at multiple levels (Rosenthal et al., 2006; Snyder & Evans, 2006; Pintor & Sih, 2009; Bucciarelli et al., 2014). Once established, aquatic invasive species can reduce native species populations to the point of local extinction and in many cases, their eradication is not achievable (Lodge et al., 1998). The potential of invasive species to induce ecological disruptions is generally greater in aquatic systems due to two factors. First, the ease with which aquatic non-native species are transported to new locations through travel with anglers, in ballast tanks, boat hulls and the aquarium trade. Second, once introduced into a linked system of rivers, streams, lakes, and oceans, passive dispersal can facilitate their invasion (Lodge et al., 1998; Grosholz, 2002). However, there is evidence that coexisting native species can recover when invasive species are removed or when their numbers are greatly reduced (Gamradt & Kats, 1996; Bucciarelli et al., 2014). Furthermore, by studying invasive species interactions, adaptive management policies can be devised to ultimately protect ecosystems (Kats & Ferrer, 2003).

In the Santa Monica Mountains (Los Angeles, CA, USA) high-gradient, step-pool streams are impacted by a variety of invasive species including the red swamp crayfish (*Procambarus clarkii* Girard, 1852), American bullfrog (*Rana catesbeiana* Shaw, 1802), and mosquitofish (*Gambusia affinis* Baird & Girard, 1853) (Gamradt & Kats, 1996; Lawler et al., 1999; Chin, 2002; Kats & Ferrer, 2003; Bucciarelli et al., 2014). The introduction of these non-native species has led to a decline in native species populations, including the California newt (*Taricha torosa* Stebbins & McGinnis 2012), which is recognized as a Species of Special Concern (Hayes & Jennings, 1986; Gamradt & Kats, 1996; Lawler et al., 1999; Kats & Ferrer, 2003; Schloegel et al., 2009). The red swamp crayfish is a globally introduced invasive species that has established populations throughout the Santa Monica Mountains, from its native range in the southern United States that extends as west as Texas, east to Alabama, and north to southern Illinois along the Mississippi River (Riley et al., 2005; Gherardi, 2007). The red swamp crayfish is not only a problematic predator of native amphibian species, like the California newt, Pacific tree frog (*Pseudacris regilla* Hallowell, 1854) and California tree frog (*Pseudacris cadaverina* Cope, 1866), but it is also recognized as an ecosystem engineer capable of shaping the abiotic conditions in its habitat (Statzner et al., 2003; Moore, 2006; Rosenthal et al., 2006; Gherardi, 2007).

Over the last 10 years, the New Zealand mud snail (*Potamopyrgus antipodarum* Grey, 1853) has been introduced to the Santa Monica Mountains, most likely as eggs transported on footwear. New Zealand mud snails can consume the majority of food resources available in an area, which can result in a reduction of native mollusk and invertebrate species (Alonso & Castro-Diez, 2008; Hibbs et al., 2012). Because *P. antipodarum* is parthenogenic and ovoviviparous, it is able to invade and rapidly expand its distribution (Gerard et al., 2017), thereby altering ecosystem functions by means of population numbers that can exceed $\sim$ 500,000/m^2 (Richards et al., 2001; Hershler et al., 2010). In other systems, researchers have found that Brachycentridae, Ephemerellidae, Baetidae, and non-chironomid Diptera dominate areas without NZMS, but are almost wholly absent in areas colonized by *P. antipodarum* (Kerans et al., 2005). Due to its small size and reproductive success, there are few methods to control the proliferation of *P. antipodarum* once they have been introduced and populations are established.

As a mechanism to deter predation, many species have evolved unique chemical defenses (Brodie et al., 2005). These chemical defenses can influence the behavior of sympatric community members and induce changes in browsing, foraging and reproductive behaviors (Elliott et al., 1993; Elkin & Baker, 2000; Juliano & Gravel, 2002; Koch et al., 2007; Hay, 2009). These chemical cues can also indirectly affect ecosystem function by altering conspecific, predator, and prey behavior (Elliott et al., 1993; Koch et al., 2007; Hay, 2009). The California newt (*T. torosa*) produces a neurotoxin, tetrodotoxin (TTX), that functions as a chemical defense and as a chemical cue at higher and lower trophic levels (Mosher et al., 1964; Elliott et al., 1993; Brodie et al., 2005; Bucciarelli & Kats, 2015). Previous studies have demonstrated that *T. torosa*'s chemical defenses play a key role in changing the behavior of species across multiple trophic levels that in turn directly affects ecological processes (Elliott et al., 1993; Bucciarelli & Kats, 2015). For example, significantly lower numbers of macroinvertebrates have been found in areas with newts compared to areas with frogs, which appears to be the result of newt chemical cues that contain TTX, not predation (Bucciarelli & Kats, 2015). In general, TTX from aquatic newts effuses into the water as a byproduct of chemical defenses, likely due to the fact that TTX is highly water-soluble and the poison glands are concentrated in the skin. The toxin has been quantified to be released at a rate of 5×10^{13} mol/s/

cm^2 from the skin surface of *T. torosa* (Zimmer et al., 2006).

The invasion of *P. antipodarum* into local streams where *T. torosa* breed provides a unique system to analyze the potential effects of newt chemical defenses on the behavior of a relatively new invasive species. Given how recently *P. antipodarum* were introduced, it is possible that native macroinvertebrates are adapted to the seasonal presence of *T. torosa* chemical cues and invasive *P. antipodarum* are not. Therefore, the presence of *T. torosa* may slow the spread of *P. antipodarum* in streams by altering movement behavior. We hypothesized that *T. torosa* chemical cues and TTX could slow *P. antipodarum* movement and conducted two studies to test this hypothesis. The first study was completed in the laboratory to assess *P. antipodarum* movement in response to newt chemical cues and TTX. The second experiment was conducted in a natural stream to determine if *P. antipodarum* movement is affected by the presence of chemical cues from *T. torosa* and a native tree frog, the California tree frog (*P. cadaverina*).

Methods

Animal collection and laboratory experimental procedures

We conducted two separate experiments in the laboratory. The first experiment generally tested if TTX elicited any behavioral response from *P. antipodarum*. As a follow-up to this study, we conducted a second bioassay in the laboratory to assess the behavioral response of *P. antipodarum* (distance moved) when exposed to newt chemical cues relative to other amphibian cues. We ultimately chose to quantify the effects of newt chemical cues that contain TTX from *T. torosa* versus non-TTX producing amphibians to determine if TTX in conjunction with other amphibian cues affected *P. antipodarum* behavior.

New Zealand mud snails, *T. torosa*, and *R. catesbeiana* were collected by hand in the week preceding the trials. This frog species was chosen as an additional biological control to provide an alternative source of amphibian chemical cues and because it is a predatory amphibian like *T. torosa* that does not naturally coexist with *P. antipodarum*. Wild *P. antipodarum* were collected from Medea Creek (Los Angeles County, CA, USA) where no population of *T. torosa* occurs. As a result, the collected *P. antipodarum* presumably would not have previously been exposed to TTX. To our knowledge, California newts have never populated this stream and certainly have not been present since the time New Zealand mud snails invaded the area. Two adult *T. torosa* (snout-vent length: $\bar{x} = 6.1$ cm, mass: $\bar{x} = 9.7$ g) were collected from Cold Creek Preserve (Los Angeles County, CA, USA) and one *R. catesbeiana* (mass = 28.7 g) was collected from Malibu Creek (Los Angeles County, CA, USA) for subsequent production of newt and amphibian chemical cue solutions.

We assessed the effect of TTX on *P. antipodarum* movement using acrylic mesocosms (10 cm × 7 cm) placed on a 1 cm^2 grid filled with a TTX solution at a concentration of 300 nmol TTX × l^{-1}. We selected this concentration because it falls within a range previously measured and consistently observed in local wild *T. torosa* populations (Zimmer et al., 2006; Bucciarelli & Kats, 2015; Bucciarelli et al., 2016). Mesocosms were filled with either 100 ml of TTX solution or control stream water. After the mesocosm was filled, three *P. antipodarum* were randomly placed inside the mesocosm and remained in the solution for a 12-h period. Photos were taken at the start and at 1-h intervals for the duration of the trial resulting in a total of 13 photos for each replicate. In total, six control and six TTX replicates were completed. The photos were analyzed and percentage of movement calculated by determining the percentage of snails that moved during each 1-h period. Percentages were then averaged over the duration of the experiment, arcsine log-transformed, and these values used for statistical analysis.

The effect of newt chemical cues on *P. antipodarum* movement was tested with the same experimental setup, but filled with one of the four experimental solutions. These solutions consisted of two batches of newt and two batches of bullfrog solutions. The first batch of newt solution was prepared by soaking two newts in 1 l of Cold Creek stream water for 60 min [Zimmer et al. (2006); quantitated TTX concentration ~ 1 nmol TTX × l^{-1} via high-performance liquid chromatography (Bucciarelli et al., 2014)]. The second solution was prepared and TTX concentration quantitated following the same protocol, but newts were soaked for

120 min (TTX ~ 3 nmol TTX × l^{-1}). Both bullfrog solutions were prepared just as newt solutions, but an adult *R. catesbeiana* was used in place of *T. torosa* and soaked for 60 min. A total of two 1 l batches of bullfrog solution were made. All solutions were created using water collected from a stretch of Cold Creek devoid of *T. torosa*. Each batch was prepared and immediately used.

Mesocosms were filled with 100 ml of one of the four solutions: newt 60-minute solution, newt 120-minute solution, bullfrog solution, or stream water, which served as a control. After the mesocosm was filled, 4 *P. antipodarum* were placed inside, one at each cardinal direction. Based upon snail behavioral responses in our previous experiment, *P. antipodarum* were left in the solution for a 1-h period. Photos were taken at the beginning of the 1-h period and at 10-min intervals for the duration of the hour, resulting in a total of seven photos for every replicate. A total of 12 replicates were completed for each experimental solution.

Using the grid that was placed under each mesocosm, we measured the individual movement of *P. antipodarum* in each 10-min period by marking their position from photographs on the grid and measured by-hand the distance between each position. The individual movement of the four snails in a mesocosm was averaged and the resultant values used as the response variable in our statistical model.

Field experiment

The effect of *T. torosa* chemical cues on *P. antipodarum* was assessed in a natural stream by comparing *P. antipodarum* movement in the presence of *T. torosa* or *P. cadaverina*. Field trials were conducted at Medea Creek (Los Angeles County, CA) because the streambed is primarily flat and flow velocities remain relatively slow throughout much of the year (~ 2–5 cm^{-s}). Throughout the stream, experimental 10 cm^2 open areas were located and marked with colored aquarium gravel at each corner. Adult *T. torosa* (snout-vent length: $\bar{x} = 6.4$ cm; mass: $\bar{x} = 10.0$ g) and *P. cadaverina* (mass: $\bar{x} = 4.9$ g) were collected by hand from an adjacent creek because neither species inhabits Medea Creek. We used *P. cadaverina* as a control rather than an empty container because their presence controlled for movement in the container and non-TTX amphibian cues that may affect *P. antipodarum*. Additionally, *P. cadaverina* rather than *Rana catesbeiana* was used during field experiments because no bullfrogs occur at Medea Creek. To prevent a possible introduction of *R. catesbeiana*, we, therefore, utilized the native *P. cadaverina* for this experiment in the event that animals escaped their enclosures.

Mesh containers housing *T. torosa* or *P. cadaverina* were placed directly upstream of the marked experimental area. Unlike laboratory assays where snails could not move away from sources of chemical cues, this design created an area under the constant influence of either animal's chemical cues but did not constrain *P. antipodarum* behavior. The total number of New Zealand mud snails present in the marked area and the number of New Zealand mud snails moving inside of the marked area were recorded at 15-min intervals for 120 min (a total of 8 time points). Thus, snails moving away from cue sources would vacate areas and movement away from point sources of *T. torosa* or *P. cadaverina* cues would result in fewer snails in the area.

To quantify potential behavioral differences between snails within frog and newt experimental areas, we evaluated the mean percent movement and percent change in the number of snails in an experimental area. To calculate the mean percent movement of snails in an experimental area, for each of the eight time points, we divided the number of moving snails by the total number of snails present then averaged the percent values. This process yielded a mean percent movement for each of the 12 trials. To calculate the percent change in snails, we evaluated the percent change between the initial and final number of snails within an experimental area to derive a positive or negative percent change. Hence, an initial and final count of 15 and 20 snails in an experimental area would result in a + 0.25, whereas an initial and final count of 20 and 15 snails would equal − 0.25. All values were arcsine log-transformed before statistical analysis. All experimental frogs and newts, mesh containers, and gravel were removed from Medea Creek and animals were returned to where they were originally collected.

Statistical analysis

With the transformed data from the laboratory TTX bioassays, we performed a paired student's *t*-test to determine if percent movement in TTX solution differed from controls. Using the data from the second laboratory experiment that utilized newt and bullfrog solutions, we tested for potential differences in movement between the four treatments. To do this, we created a linear model in the *R* framework using the *lm* function fitted with snail movement data and treatment group. The results of this model were analyzed using the *anova* function. Potential differences between groups were compared with a Tukey's Honest Significant Difference test using the function *TukeyHSD* with $a = 0.05$.

To assess if the movement and the number of snails differed in our stream experimental areas, we performed two tests to evaluate potential differences in (1) the mean percent of individuals moving in each area and (2) the percent change in the number of snails. For both comparisons, a student's *t* test was used to determine if the two metrics significantly differed.

Results

Laboratory experiment

We found that a significantly lower percentage of *P. antipodarum* moved when exposed to the TTX solution ($P < 0.001$). Overall, the mean percent movement in the TTX solution was reduced by approximately fivefold (TTX:$\bar{x} = 0.13$ percent ± 0.02 S.E.M.; $\bar{x}$ *Control*: 0.63 percent ± 0.04 S.E.M.; see Fig. 1). The results of our analysis of variance to compare snail movement in the four experimental solutions indicated that *P. antipodarum* on average moved significantly less when exposed to amphibian solutions ($F = 48.26$; $df = 3$, $P < 0.001$). When we compared the means of each group, *P. antipodarum* in both newt solutions moved significantly reduced distances relative to snails in amphibian (Newt120-Amphibian: $P < 0.001$; Newt60-Amphibian: $P < 0.001$) and control solutions (Newt120-Control: $P < 0.001$; Newt60-Control: $P < 0.001$, Fig. 2a, b). However, there was no significant difference in snail distance moved between the two newt solution treatments (Newt120-Newt60: $P = 0.74$). Across the 10-min interval periods, *P. antipodarum* in the newt 120-minute solution moved on average 2.7 cm (± 0.08 S.E.M.), in the newt 60-minute solution 2.5 cm (± 0.08 S.E.M.), in the bullfrog solution 3.4 cm (± 0.09 S.E.M.), and in the control 3.8 cm (± 0.08 S.E.M.; Fig. 2a, b).

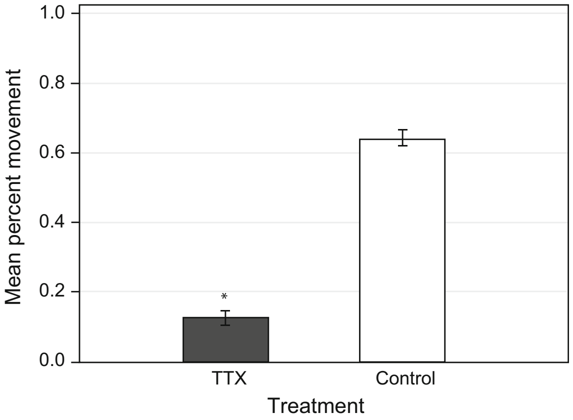

Fig. 1 Mean percent movement of *P. antipodarum* was reduced fivefold in TTX solution compared to controls. The mean measured movement was 13% in the experimental TTX solution compared to 63% in the control solution

Field experiment

In the stream, we found that *P. antipodarum* in experimental areas downstream of *T. torosa* moved a significantly higher percent relative to *P. cadaverina* ($t = -6.63$; $df = 10$, $P < 0.001$). The mean percent snail movement in the presence of *T. torosa* was 0.19 and 0.04 in the presence of *P. cadaverina* (Fig. 3a). The percent change in number of snails inside experimental areas was not significantly different between treatments ($t = 1.98$; $df = 10$, $P = 0.075$). Overall, the mean percent change in the number of snails decreased ∼ 13% in the presence of *T. torosa* and increased ∼ 2% in the presence of *P. cadaverina* (Fig. 3b).

Discussion

Overall, TTX and newt solutions had the greatest effect on New Zealand mud snail movement behavior. The results of our laboratory experiments show that *P. antipodarum* is affected by ecologically realistic concentrations of TTX. *Potamopyrgus antipodarum* significantly reduced its movement in the presence of TTX and solutions that contained newt chemical cues (Fig. 1). Specifically, we found that snails exposed to

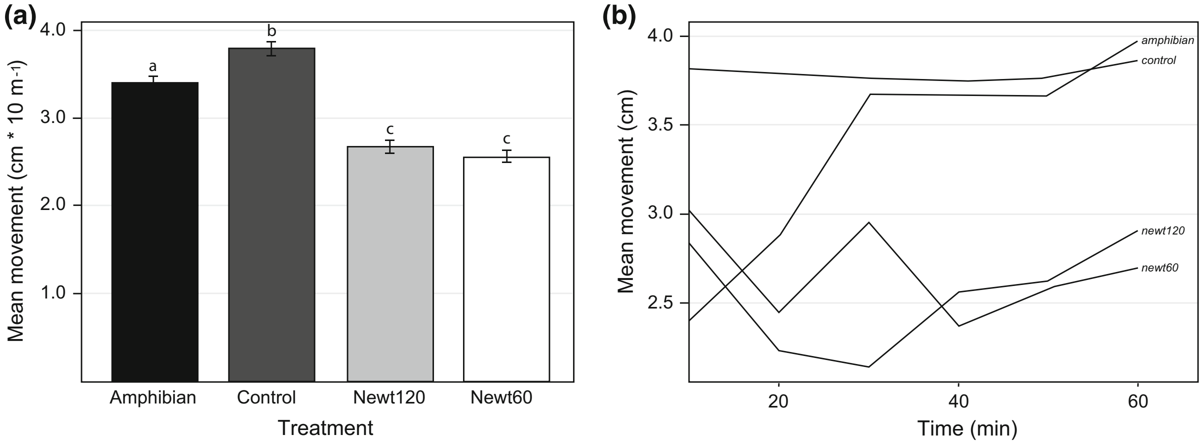

Fig. 2 **a** Mean movement of *P. antipodarum* is reduced when exposed to newt experimental solutions. Mean movement of snails in control solutions was ~ 70% greater compared to snails in 120-minute newt and 60-minute newt solutions. Results indicated significant differences in movement between groups (ANOVA, $P < 0.001$) but not between snails in both newt solutions (Tukey HSD, $P = 0.74$). **b** Mean movement of *P. antipodarum* at each 10-min period shows the significantly reduced movement of snails in newt chemical cue solutions

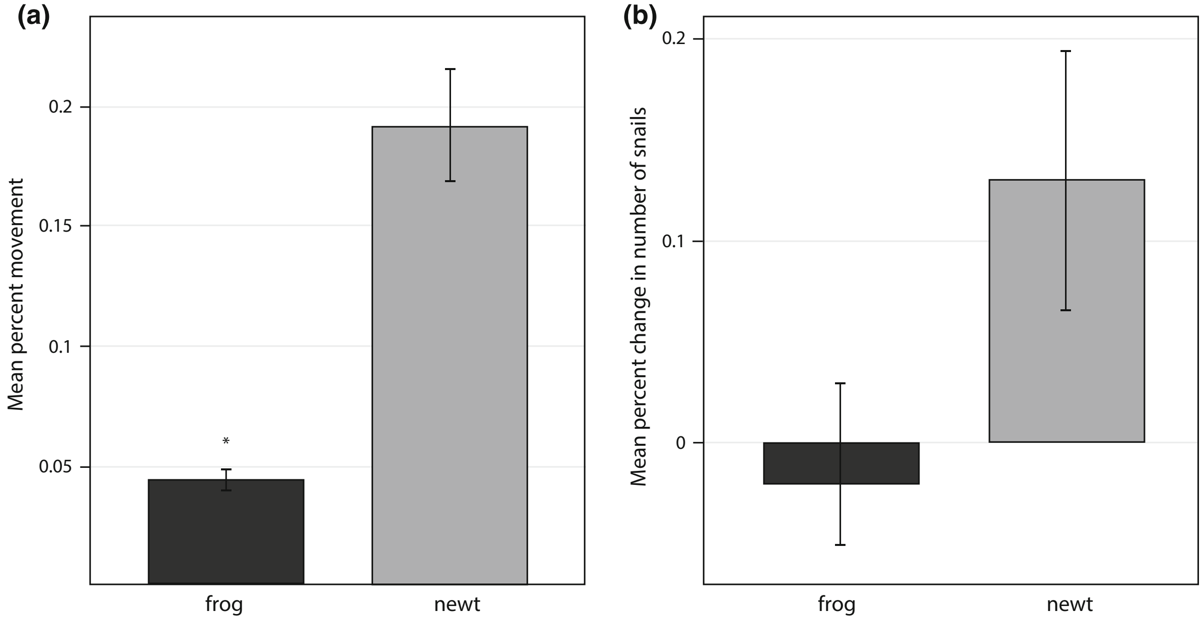

Fig. 3 **a** The percentage of snails moving within experimental areas. In proximity to newts, *P. antipodarum* moved ~ 4 times as much compared to snails near *P. cadaverina*. Graph (**b**) shows the mean total change in the number of *P. antipodarum* present inside of our experimental areas. These results suggest that snails move to avoid areas where they would contact newt chemical cues

TTX moved an average half the distance of snails in control solutions and one-third the distance of snails in an amphibian chemical cue solution. The difference between the amphibian cue and newt solutions demonstrates that TTX may be an ecologically interesting factor affecting *P. antipodarum* behavior independent of any effects caused by the presence of other amphibians. These results suggest that newt chemical cues, and specifically TTX, elicit a behavioral change in *P. antipodarum*. Other studies have found that chemical cues from higher trophic level organisms can affect the movement of species at lower trophic levels. Specifically, fish odors were found to affect night-time drift behavior of mayflies in streams (McIntosh & Peckarsky, 1996). Similar responses have been observed in marine systems where nudibranchs elicit anti-predator behavior in sea anemones (Howe & Sheikh, 1975).

Under natural conditions, however, we found that *P. antipodarum* moved at a significantly greater amount when snails were in close proximity to newts relative to snails that were near native tree frogs. Specifically, over time we found that fewer *P. antipodarum* remained within experimental areas downstream of *T. torosa* compared to areas with *P. cadaverina* frogs. These results indicate that over time *P. antipodarum* are moving more in the presence of newt chemical cues and imply that *P. antipodarum* is moving more to avoid sources of newt chemical cues and TTX. It is important to note that our field experiment only tested the effect of *T. torosa* chemical cues under one specific set of natural conditions and different conditions could alter the effect of newt chemical cues (Camargo & Ward, 1992). However, given the slow flow rates ($\sim$ 1–5 cm s^{-1}) of these arid and ephemeral streams, it is likely dispersal of chemical cues is similar throughout much of the year.

We observed a difference in movement behavior of *P. antipodarum* between laboratory and field experiments that may be explained by differences in exposure between environments. Mesocosms in our laboratory experiment were closed systems that exposed *P. antipodarum* to a sustained, higher concentration of TTX and newt chemical cues than they would have experienced under field experimental conditions. Additionally, in the field, experimental areas were open, and as result, *P. antipodarum* had the ability to move away from the source of newt chemical cues, unlike the laboratory mesocosms. In fact, laboratory snails in experimental solutions did not stop moving entirely, which may have been an effort to move away from newt and TTX solutions (Fig. 2). It is also possible that snails were sub-lethally poisoned by TTX and newt solutions in our laboratory experiment that resulted in reduced movement. Bucciarelli & Kats (2015) observed that the strike velocity and angular velocity of predatory dragonfly nymphs (*Anax junius*) were reduced in the presence of TTX, but it was not clear whether this was because TTX elicited such a behavioral response or nymphs were sub-lethally poisoned by the neurotoxin. Moreover, other invertebrates exposed to fish odors responded differently based on the risk of predation (McIntosh & Peckarsky, 1996). With regard to our study, this factor seems unlikely to have had an effect since neither species is locally known to feed on New Zealand mud snails.

Overall, our results indicate that a native amphibian may play some role in limiting the spread of an invasive species and, as a result, could help to limit the ecosystem impacts of *P. antipodarum*. Our results show that New Zealand mud snails are affected by TTX and under natural conditions, snails appear to avoid California newts. The persistence of healthy populations of *T. torosa* via the removal of invasive species like *P. clarkii* should continue as novel effects of newt chemical cues and the ecological role of TTX are further investigated (Gamradt & Kats, 1996; Kats & Ferrer, 2003). By protecting native *T. torosa* populations, it may be possible to maintain valuable ecosystem services provided by a native species that seemingly indirectly could impede the spread of a non-native species currently difficult or impossible to eradicate. Further studies on the benefits that native amphibians provide in ecosystems, with hope will provide land managers with novel approaches to managing non-native species.

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